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Temporal and spatial variability of phytoplankton in Lake Poyang: The largest freshwater lake in China

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ABSTRACT

The composition and both the temporal and spatial distribution of phytoplankton were studied in Lake Poyang; samples were collected every 3 months from January 2009 to October 2011 at 15 sites. The phytoplankton community was found to belong to seven groups, with Bacillariophyta dominating. No significant difference was observed in the phytoplankton community structure at any of the sites ($p = 0.2371$), except one site; however, the structure was significantly different with regard to annual and seasonal trends ($p = 0.0001$ and $p < 0.0001$, respectively). *Aulacoseira granulata*, *Synedra acus*, *Fragilaria virescens*, and *Cryptomonas erosa* were the main contributors to the dissimilarity in temporal distribution. Although the nutrient concentrations for 3 years combined were relatively high (mean total nitrogen was 1.719 mg L^{-1} and mean total phosphorus was 0.090 mg L^{-1}), phytoplankton biomass was low (mean total biomass of 0.203 mg L^{-1}). The underwater light condition, as indicated by the Secchi depth, was shown to be the principal limiting factor in regulating the growth of phytoplankton, and the transparency coincided with biomass variation on a seasonal level. The effect of nutrients on phytoplankton may be concealed by the water level, which varied over a wide range among different seasons. However, the annual trend for the biomass was associated with the nutrient concentration, which increased yearly and initiated the development of phytoplankton. The biomass is high in the south and low in the north, which may be the result of greater underwater light climate and high nutrient concentrations in the southern area.

Introduction

Phytoplankton is important for providing the foundation for aquatic food chains (Reynolds, 1984a, b) and has attracted great attention worldwide. To adequately understand the life cycle of phytoplankton and how the phytoplankton community responds to ecological change, researchers have investigated the distribution of phytoplankton, both temporally and spatially, in various bodies of water for nearly a century (Chen et al., 2003; Dokulil and Padisak, 1994; Reynolds, 1984a; Valdes-Weaver et al., 2006). On some level, alterations in phytoplankton species composition and biomass in a water body reflect a changing environment and indicate the trophic status (Cottingham and Carpenter, 1998; Paerl, 1988; Reynolds et al., 1993). Therefore the patterns of the phytoplankton community provide a possible method for evaluating ecological alterations in response to stressors that damage the system, such as an increase in nutrients.

Lake Poyang (28°22′–29°45′ N,115°47′–116°45′ E), which is downstream of the Yangtze River, is the largest freshwater lake in China, with a watershed area of 1.622×10^5 km^2. Annual discharge of the lake is approximately 1.457×10^{11} m^3, which accounts for 15.6% of the average Yangtze River runoff. The storage capacity of Lake Poyang is approximately 2.95×10^{10} m^3, which is 5.9 times higher than that of Lake Taihu, the third largest freshwater shallow lake in China (Chen et al., 2003; Zhu and Zhang, 1997). Lake Poyang contains five inflows, including the Ganjiang River, Fuhe River, Xinhe River, Xiushui River, and Raohe River and freely exchanges water with the Yangtze River in Hukou (Fig. 1) (Fu et al., 2003; Wang et al., 2011). The water level varies over a wide range in different seasons, depending on the balance between the Yangtze River and Lake Poyang, and rainfall in the local area also has an impact (Shankman et al., 2006; Zhu and Zhang, 1997). As the largest freshwater lake in China, Lake Poyang provides resources for local economic development, although multiple stressors from human actives and abiotic factors are imposed on the lake's ecosystem. Accordingly, the availability of continuous and long-term water quality monitoring is essential for protecting this ecosystem. In 2008, the Poyang Lake Laboratory for Wetland Ecosystem Research

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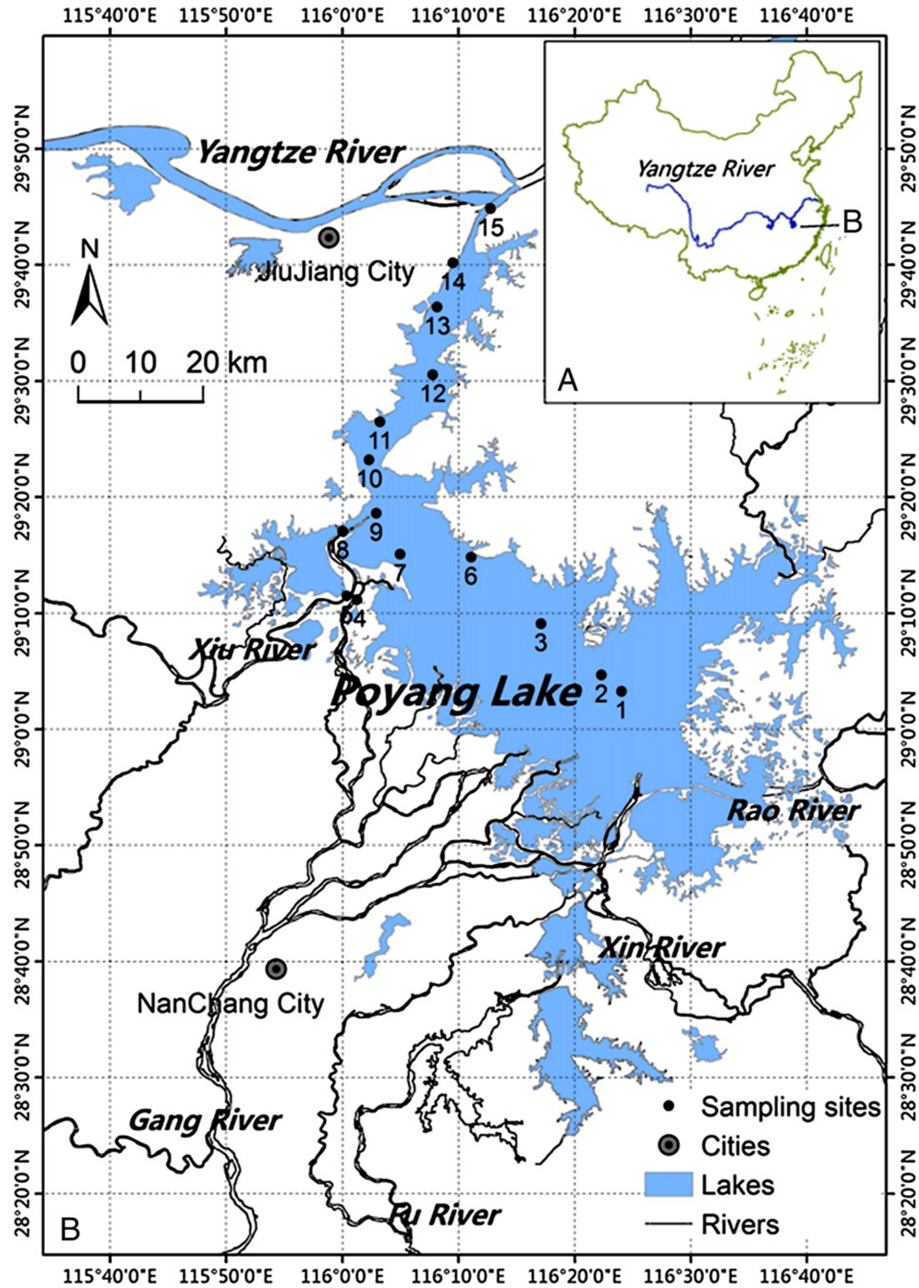

Fig. 1. Location of Lake Poyang, China and the sampling sites.

was built to monitor the baseline environmental conditions in Lake Poyang and to discover patterns and establish primary conclusions regarding the factors affecting this environment.

However, few data (Supplementary information Table 1) exist regarding the phytoplankton community in Lake Poyang (Wang et al., 2004; Xie et al., 2000). Previous phytoplankton studies carried out in the 1980s and 1990s have limited spatial and temporal coverage. Furthermore, there is limited information in the literature on the factors limiting phytoplankton growth in Lake Poyang, even though such factors, including the nutrient, light, temperature, and grazing levels, are widely studied in aquatic ecosystems (Reynolds, 1984a; Vanni and Temte, 1990).

The primary objective of this study was to illustrate the temporal and spatial distribution of the phytoplankton composition and biomass in Lake Poyang. Additionally, we also considered the environmental factors that are responsible for alterations in phytoplankton composition and biomass. Our research on phytoplankton in Lake Poyang is important for providing original and relatively long-term information for future studies, in addition to potentially providing a means to detect environmental changes in Lake Poyang.

Materials and methods

Sample collection and lab analysis

Sampling was conducted four times a year (winter = January; spring = April; summer = July; and autumn = October) from January 2009 to October 2011 at 15 sites (Fig. 1) within Lake Poyang. Although the surface area of Lake Poyang changes greatly in different seasons, these 15 sampling sites are all covered with water throughout the entire year.

Vertically integrated water samples were obtained and placed into acid-cleaned 10-L plastic containers, and kept cool and shaded before being transported to the laboratory. Environmental parameters, including pH, water temperature, dissolved oxygen, turbidity, and electrical conductivity were measured using a Hydrolab Datasonde 5 sensor in situ. The water transparency was determined using a Secchi disk. The suspended solids (SS), chemical oxygen demand (COD_{Mn}), chlorophyll *a*, and nutrient concentrations (TN, TP, DTN, DTP, NO_2–N, NO_3–N, NH_4–N, and PO_4–P) were analyzed according to APHA (1998).

Phytoplankton samples were fixed with Lugol's iodine solution (1% v/v) and allowed to settle for 48 h prior to counting using a microscope (Chen et al., 2003); the taxa identification was performed according to Hu and Wei (2006). Because the biomass in Lake Poyang was low, we counted all phytoplankton cells in a 0.1-mL fixed sample that was concentrated from 1 L to 30 mL so as not to miss species. Mean cell volume was calculated using appropriate geometric configurations (Hillebrand et al., 1999). Volume values were converted to biomass assuming that 1 mm^3 of volume was equivalent to 1 mg of fresh-weight biomass (Chen et al., 2003).

Data analysis

To detect relationships between environmental factors and phytoplankton biomass, the data were averaged by year and season temporally and by site spatially and were compared to the corresponding average Secchi depth, which was representative of underwater light conditions, and the dissolved nutrient (DTN and DTP) concentrations.

All statistical analyses were performed using PAST software (Paleontological Statistics v2.15) (Hammer et al., 2001), with the exception of Spearman's correlation which was performed using the statistical package SPSS for Windows (version 17.0). We employed nonparametric statistics because the lack of parameter normality precluded parametric statistical testing. Significance analyses for environmental factors and phytoplankton biomass, on both temporal and spatial levels, were performed using Kruskal–Wallis nonparametric tests. An analysis of similarity (ANOSIM) was used to examine alterations in community species composition (Clarke, 1993). More details can be found in Gillett and Steinman (2011). Furthermore, if a significant difference in species composition was found for two or more groups, we determined taxa that could be responsible for the difference using the similarity percentage (SIMPER) procedure based on the phytoplankton biomass data.

Table 1
Environmental variables summarized as mean values and ranges for all 12 samplings at 15 sites in Lake Poyang, China, from 2009 to 2011.

Variable	Units	Mean	Range
Water transparency	m	0.37	0.04–1.10
Turbidity	NTU	75.06	5.1–410
Suspended solids	mg L^{-1}	116.02	5.75–2990.57
Temperature	°C	18.54	3.89–32.12
pH		7.74	6.85–8.89
Conductivity	μS cm^{-1}	148.4	56.1–780
Dissolved oxygen	mg L^{-1}	8.24	4.3–15.9
COD_{Mn}	mg L^{-1}	2.90	1.21–13.01
TN	mg L^{-1}	1.76	0.69–4.21
TP	mg L^{-1}	0.092	0.017–0.46
NO_3–N	mg L^{-1}	0.67	0.062–1.78
NO_2–N	mg L^{-1}	0.022	0–0.11
NH_4–N	mg L^{-1}	0.58	0.029–2.18
PO_4–P	mg L^{-1}	0.018	0–0.27
Chlorophyll *a*	μg L^{-1}	5.11	0–25.57

Results

Environmental conditions

Data from 15 sampling sites between 2009 and 2011 were examined. The results of the overall environmental variables are presented in Table 1. The Secchi depth was quite low in Lake Poyang, with a mean value of 0.37 m; 80% of the Secchi depth measurements were below 0.5 m. The average concentrations of turbidity and suspended solids were quite high, with the mean value of 75.06 NTU and 116.02 mg L^{-1}, respectively. The nutrient concentrations for 3 years were relatively high (mean total nitrogen was 1.719 mg L^{-1} and mean total phosphorus was 0.090 mg L^{-1}).

Seasonally, the Secchi depth increased from winter (0.29 m) through summer (0.52 m) and then dropped to 0.27 m in autumn (Fig. 2). In contrast, the dissolved nutrient concentrations peaked in winter, decreased from winter to summer, and then increased in autumn (Fig. 2).

There was a slight, but insignificant, reduction in Secchi depth of approximately 4 cm for the mean value from 2009 to 2011 (Fig. 3). Conversely, the dissolved nutrient concentrations exhibited a pronounced inter-annual variation (Fig. 3). In comparison with 2009, the concentrations of DTN and DTP in 2011 increased by 0.56 and 0.026 mg L^{-1}, i.e., by approximately 47% and 78%, respectively, and the inter-annual difference was significant for DTN ($p < 0.001$) and DTP ($p < 0.05$). In general, the Secchi depth reflected a decreasing trend from the southern to northern regions of Lake Poyang (Fig. 4) that was similar to the pattern observed for DTN and DTP, which were highest in Site 1.

Phytoplankton composition

In total, 54 genera belonging to seven phytoplankton groups were identified during the 3-year monitoring period (Supplementary information Table 2). Chlorophyta (26) were the most important group, representing 48.1% of the total number of genera, followed by Bacillariophyta (13), Cyanobacteria (6), Euglenophyta (4), Cryptophyta (2), Dinophyta (2), and Chrysophyta (1). The temporal and spatial distribution of the proportions of different phytoplankton groups from January 2009 to October 2011 is shown in Fig. 5, as determined according to biomass data. The Bacillariophyta *A. granulata*, *S. acus*, and *Fragilaria virescens*, which were the dominant species, accounted for at least 50% of the total biomass in most of the 12 samplings and 15 sites and thus comprised the most dominant group with regard to biomass. On average, each of these species accounted for more than 10% of the phytoplankton biomass (Table 2). In addition to Bacillariophyta, Cryptophyta and Chlorophyta were also important phytoplankton groups in the phytoplankton biomass of Lake Poyang (biomass: Bacillariophyta > Cryptophyta > Chlorophyta). The Chrysophyta observed was *Dinobryon sertularia*.

Seasonal variation

Significant seasonal variability was recorded in the community structure and total phytoplankton biomass ($p = 0.0187$ and $p < 0.0001$, respectively). In addition, the biomass of each group, except for Bacillariophyta and Chrysophyta, also changed significantly in different seasons ($p < 0.05$). The phytoplankton biomass was significantly greater in summer than in other seasons ($p < 0.05$); i.e., at times when the transparency was elevated. The phytoplankton community structure was significantly different in different seasons ($p = 0.0001$). The species that caused the significant seasonal dissimilarity in the phytoplankton community are listed in Table 2.

Inter-annual variation

A consistent relationship was observed between the total phytoplankton biomass and mean dissolved nutrient concentrations. The phytoplankton biomass was distinctly lower in 2009 than in the subsequent 2 years in Lake Poyang (Fig. 3). Relative to 2009, the phytoplankton biomass in 2011 increased to 0.29 mg L^{-1}, which was 7.6 times higher than that in 2009. The substantial increase in the Bacillariophyta biomass was primarily attributable to this trend (accounting for 73.8% of the total biomass increase), although the Cryptophyta and Chlorophyta biomass also increased yearly in Lake

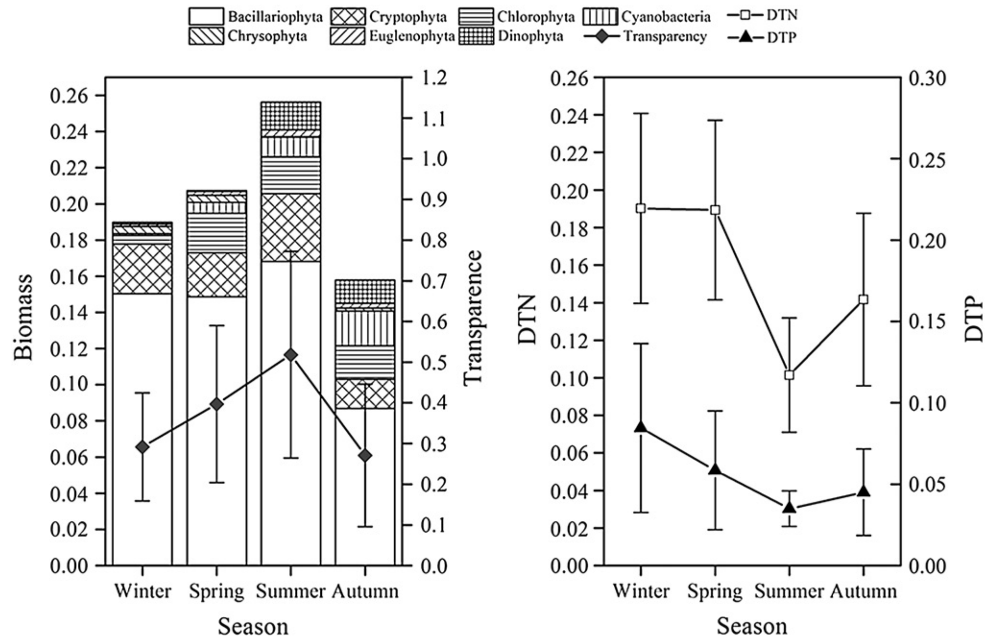

Fig. 2. Seasonal variation of the mean phytoplankton biomass (mg wet weight L^{-1}), water transparency (m), dissolved total nitrogen (DTN) (mg L^{-1}) and dissolved total phosphorus (DTP) (mg L^{-1}) in Lake Poyang.

Poyang. The phytoplankton community structure was significantly different among the 3 years ($p = 0.0001$), mainly because of *A. granulata*, *S. acus*, *F. virescens*, and *Cryptomonas erosa*, which contributed approximately 60% to the total deviation (Table 2).

Spatial variation

The mean total biomass was generally higher in the south and lower in the northern region (Fig. 4). The highest mean total biomass was measured at Site 8 (1.08 mg L^{-1}), which showed a value over 7-fold higher than that of the other sites. At Site 12, the mean total biomass was the lowest (0.27 mg L^{-1}) and was significantly different from that of most of the other sites ($p < 0.05$). The biomass of all seven groups was distinctly decreased in the northern region, particularly at Sites 12, 13, 14, and 15. The spatial difference in the phytoplankton biomass mainly resulted from spatial variations in the Bacillariophyta biomass, which (together with Cryptophyta and Chlorophyta) comprised at least 75% of the total biomass at all 15 sites. The relative biomass of Cyanobacteria and Chlorophyta exhibited inverse patterns in the northern region, as the relative biomass of the Cyanobacteria increased notably, whereas that of Chlorophyta decreased dramatically (Fig. 5). However, no distinct spatial alteration was observed for the other groups.

No significant difference was detected in phytoplankton community structure ($p = 0.2371$), except at Site 8 where the phytoplankton community was significantly different from that at Sites 1, 5, 6,

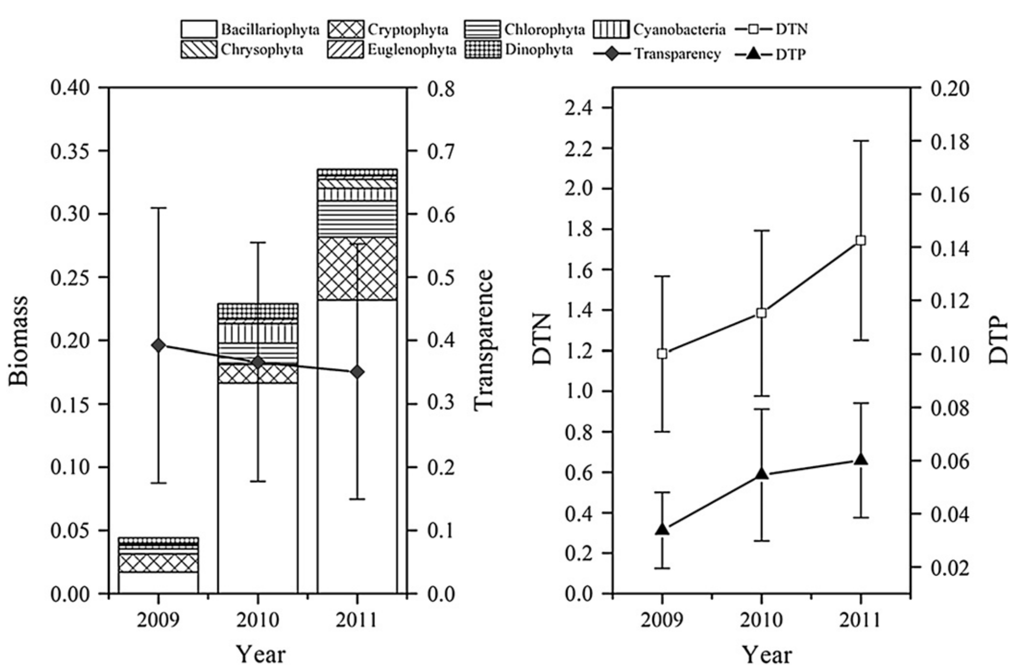

Fig. 3. Mean annual phytoplankton biomass (mg wet weight L^{-1}), water transparency (m), dissolved total nitrogen (DTN) (mg L^{-1}), and dissolved total phosphorus (DTP) (mg L^{-1}) over the three years sampling in Lake Poyang.

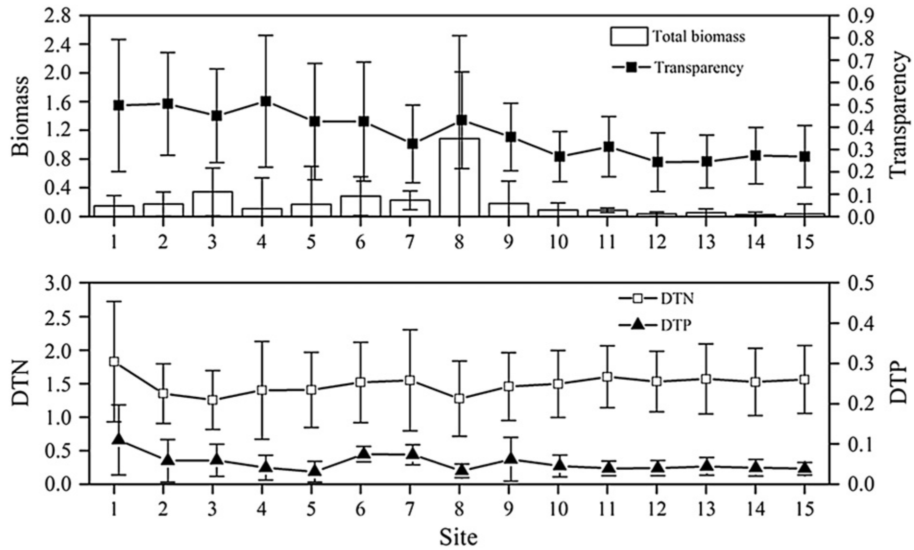

Fig. 4. Spatial distribution of the mean total phytoplankton biomass (mg wet weight L^{-1}), water transparency (m), dissolved total nitrogen (DTN) (mg L^{-1}), and dissolved total phosphorus (DTP) (mg L^{-1}) in Lake Poyang. Sites may be found in Fig. 1.

7, 10, 11, 12, 13, 14, and 15 ($p < 0.05$). *S. acus*, *A. granulata*, and *F. virescens* were the major contributors (>10%) to this dissimilarity.

Correlations between phytoplankton biomass and Secchi depth and nutrient concentrations

The correlation analysis showed a strong relationship between phytoplankton biomass and Secchi depth in Lake Poyang. With the exception of Chrysophyta, the total phytoplankton biomass and biomass of the other six groups were significantly ($p < 0.05$) and positively correlated with the Secchi depth. With regard to the impact of nutrient effects on phytoplankton biomass, correlations between biomass and the concentrations of DTN and DTP were also assessed (Table 3). The DTN concentration was significantly ($p < 0.05$) and inversely related to the total biomass and biomass of three groups (Chlorophyta, Cyanobacteria, and Dinophyta). However, there were no significant correlations between the concentration of DTP/total biomass and the biomass of most groups.

Furthermore, we averaged the data by year and season and found that the transparency was also significantly and positively correlated with the biomass of the major groups (i.e., Bacillariophyta, Cryptophyta, and Chlorophyta) and the total biomass. Similar to the results above, the nutrient concentrations were not significantly related to phytoplankton biomass on a seasonal level in which the data were averaged by year. Annually, the DTN concentration was significantly and positively related to the Bacillariophyta biomass, i.e., the major biomass contributor. In addition, the relationship was significantly positive between the DTP concentration/total biomass and the biomass of the three major groups (Bacillariophyta, Cryptophyta, and Chlorophyta).

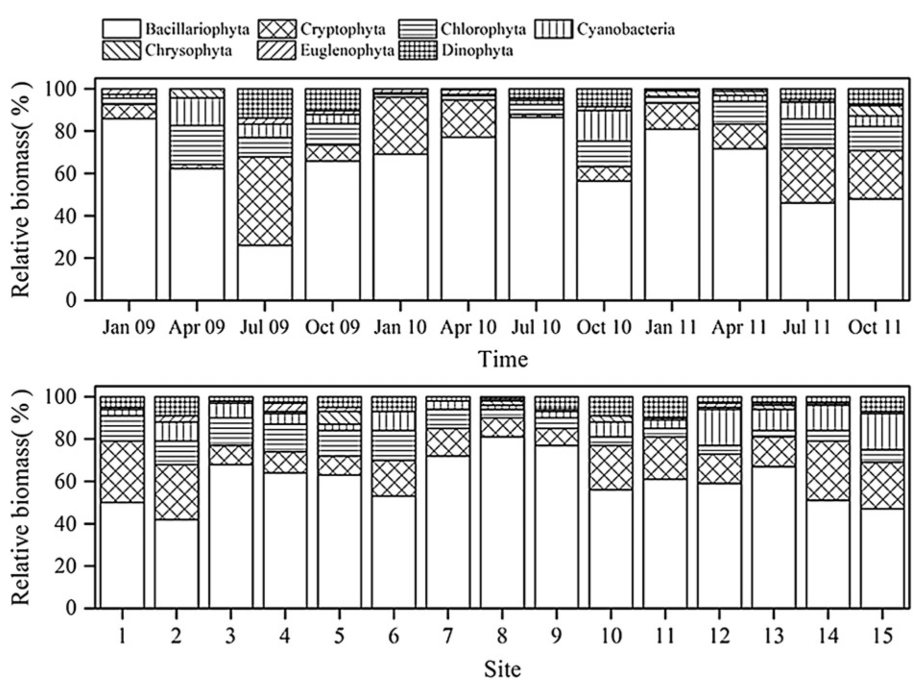

Fig. 5. Temporal and spatial variation of relative phytoplankton composition in seven algal groups in Lake Poyang. Sites may be found in Fig. 1.

Table 2
Percentage of phytoplankton taxa that account for at least 1% of the average biomass from 2009 to 2011 and contribution to differences in the community structure on annual and seasonal levels in Lake Poyang.

	Species	Percentage	Contribution (%)	
			Annual	Seasonal
Bacillariophyta	*Aulacoseira granulata*	28.58[a]	31.17	29.12
	Synedra acus	16.61[a]	9.361	9.42
	Fragilaria virescens	15.99[a]	9.07	9.78
	Asterionella spp.	3.47	2.55	2.37
	Surirella spp.	1.30	2.05	2.21
	Navicula spp.	1.00	1.49	1.56
Cryptophyta	*Cryptomonas erosa*	7.31	9.36	10.58
	Cryptomonas ovata	5.18	7.43	5.64
Chlorophyta	*Scenedesmus* spp.	1.23	1.34	1.45
	Eudorina spp.	1.69	1.08	1.04
	Actinastrum spp.	1.18	0.65	0.65
Cyanobacteria	*Microcystis* spp.	2.62	4.53	4.80
	Anabaena spp.	1.42	1.98	2.12
Chrysophyta	*Dinobryon sertularia*	1.22	1.36	1.28
Dinophyta	*Peridinium* spp.	2.80	4.36	4.81
Total		91.60	87.78	86.83

[a] Dominant species.

Discussion

Phytoplankton community and low biomass

Bacillariophyta absolutely predominate in Lake Poyang, and differences in the annual and seasonal trends in phytoplankton community structure are mainly caused by the diatoms (*A. granulata*, *S. acus*, and *F. virescens*). Previous studies of the phytoplankton in Lake Poyang in the 1980s and 1990s also demonstrated the dominance of the Bacillariophyta (Wang et al., 2004; Xie et al., 2000). According to the trophic state classification of OECD (1982), Lake Poyang was eutrophic in the period of 2009 to 2011. However, for phytoplankton, our observations are inconsistent with those in other eutrophic lakes. Cyanobacterial blooms, particularly *Microcystis* blooms, commonly occur in nutrient-rich freshwater systems (Lin, 1972; Liu et al., 2011; Scheffer, 2004). Padisak (1992) stated that the role of Cyanobacteria became more important with an increasing trophic level. Hutchinson (1967) has suggested that Cyanobacterial blooms are a typical feature of a eutrophic lake dominated by such algae as *Microcystis*. With a similar turbid environment, Lake Neusiedlersee experiences spring blooms dominated by Cyanobacteria (Dokulil and Padisak, 1994). For Bacillariophyta, Reynolds (1996) has suggested that the phytoplankton community is dominated by diatoms in a well-mixed water column. When vertical mixing increased, Bacillariophyta became the dominant group in Lake Tanganyika in dry seasons (Cocquyt and Vyverman, 2005). Because of the variation of the water level and the complex lake shape, the hydrology of Lake Poyang is highly variable, and contributes to Bacillariophyta dominance. In contrast to Bacillariophyta, Cyanobacteria are unable to grow in turbulent systems (Reynolds et al., 1983). Furthermore, as reported in many studies, diatoms dominate in typical river systems (Ha et al., 2002; Wu et al., 2011). Gosselain et al. (1994) have also cited many large and nutrient-rich rivers to illustrate the dominance of Bacillariophyta. Lake Poyang, which is connected to the Yangtze River, displays river features, particularly in dry seasons, which is consistent with its status as a diatom-dominated community.

The phytoplankton biomass in Lake Poyang is low, even though the nutrient concentration is high. We suggest that light plays an important role in regulating the growth of phytoplankton. In our study, we used Secchi depth to indicate the underwater light condition and found a mean transparency in Lake Poyang of only 0.37 m. From Secchi depth/turbidity and suspended solids data, we suggested that the euphotic zone in Lake Poyang was quite shallow. With almost the same transparency, the biomass is slightly lower than that in Lake Chapala which was determined by using chl *a* data [5.1 μg L^{-1} in Lake Poyang and 5.4 μg L^{-1} in Lake Chapala (Lind et al., 1992)]. It is well accepted that light is an important factor for algal growth because it provides energy for photosynthesis and limits phytoplankton growth in low light intensity (Harris, 1978; Herman and Luuc, 1980; Reynolds, 1984a). Dokulil (1984) reported that light transmission was affected by the turbidity of the particles suspended underwater, which change the spectral form of the light. Based on trophic status index (TSI), Carlson's method (1992) for identifying limiting factors of phytoplankton growth showed that the value of TSI (CHL)-TSI (SD) and TSI (CHL)-TSI (TP) was −18.74 and −4.4, respectively, which indicated that the growth of phytoplankton in Lake Poyang was limited by the lack of light. Indeed, Lake Poyang is a turbid lake, and the turbidity may be the result of many factors. Because of its abundant sand, Lake Poyang is heavily exploited for commercial activities, particularly for sand excavation and transportation, and water movement is also an important factor, as it causes sediment resuspension. As noted by Dou and Jiang (2003), the flow rate in Lake Poyang is greater in the northern region than in the south, which is similar to the spatial distribution of transparency. Therefore the two elements mentioned above, i.e., human activity and water movement, produce the turbid environment in Lake Poyang, which in turn results in low light conditions.

Temporal and spatial variability of phytoplankton

Seasonally, lake phytoplankton biomass coincides with lake transparency, and both have peak values in the summer and are lowest in autumn, which highlights the limiting effects of light on algal growth. Furthermore, there was a strong relationship between the biomass of total phytoplankton (and that of most of the seven groups) and the Secchi depth, which illustrates the effect of light in Lake Poyang. The DTN and DTP concentrations have the same seasonal variability

Table 3
Spearman correlation coefficients for the relationship among seven phytoplankton groups, water transparency and DTN and DTP concentrations in Lake Poyang, based on all 12 sampling data.

Biomass	All data (n = 180)			Data averaged by year (n = 60)			Data averaged by season (n = 45)		
	Transparency	DTN	DTP	Transparency	DTN	DTP	Transparency	DTN	DTP
Total	0.419**	−0.171*	0.023	0.635**	0.210	0.095	0.439**	0.234	0.500**
Bacillariophyta	0.344**	−0.081	0.043	0.500**	0.055	0.223	0.364*	0.344*	0.509**
Cryptophyta	0.348**	0.025	0.172	0.606**	−0.231	0.031	0.386**	0.218	0.347*
Chlorophyta	0.554**	−0.298**	−0.061	0.623**	−0.350**	0.044	0.647**	0.026	0.342*
Cyanobacteria	0.447**	−0.379**	−0.127*	0.345**	−0.574**	−0.020	0.215	0.178	0.426**
Chrysophyta	0.119	0.019	0.008	0.169	0.013	−0.167	0.121	0.212	0.190
Euglenophyta	0.161*	−0.132	−0.088	0.260*	−0.252	−0.100	0.365*	−0.055	0.024
Dinophyta	0.235**	−0.372**	−0.170*	0.274*	−0.651**	−0.275**	0.278	−0.145	0.130

* $p < 0.05$.
** $p < 0.01$.

and vary inversely with transparency. Regardless of whether the assessment was based on all the data or only on data averaged by year, the relationship between the biomass and dissolved nutrient concentrations was not significant. It appears that the nutrient level has no obvious effect on algae, which contrasts with the results of previous studies.

As indicated above, light is the principal limiting factor in regulating the growth of phytoplankton. Regarding nutrients, there may be two reasons for the pattern and relationship with the biomass. On one hand, nutrient status has been shown by previous studies to be less important than light in algal growth in aquatic ecosystems. Light was found to be more important for restricting phytoplankton growth than were nutrients in temperate lakes compared with trophic lakes (Lewis, 1987). Kimmel et al. (1990) noted that the attenuation of light, and not basic elements such as N and P, governed phytoplankton production in many freshwater systems. In Lake Chapala, light was found to play a more important role than nutrients because of high inorganic turbidity (Dávalos et al., 1989). On the other hand, because of the connection to the Yangtze River, the nutrient effect on phytoplankton growth on a seasonal level may also be weakened by water levels in Lake Poyang, which vary over a wide range over different seasons. Based on data from the Xingzi Hydrology Station between 2009 and 2010, the water level in Lake Poyang increased from winter (7.96 m) to summer (17.80 m) and then decreased in autumn (11.90 m). Additionally, we propose that the water level determines changes in the nutrient concentration. Some other factors, including farming activities in the spring that bring more nutrients into the lake, produced no obvious decrease in the DTN concentration in spring. By only focusing on seasonal means, the effect of nutrients on phytoplankton growth may be concealed and nutrient content may even be found to be negatively related to biomass. In summary, light is vital in regulating phytoplankton growth on a seasonal level, whereas nutrients become less important or their effect may be concealed by the water level.

Although light limits the growth of phytoplankton in Lake Poyang, nutrients, as the basic chemical elements for algal growth, initiate the development of phytoplankton on an inter-annual level. In fact, we observed consistent annual trends for changes in the biomass and nutrient concentrations. The transparency had a slight reduction from 2009 to 2011, which eliminated the role of transparency on an annual level. From 2009 to 2011, DTN and DTP increased from 1.18 to 1.74 and 0.034 to 0.060 mg L^{-1}, respectively. It is speculated that increased pollution from cities, farmland, and human actives may have caused the detected increase in nutrients. Phytoplankton biomass also rose dramatically, from 0.044 to 0.34 mg L^{-1}. In addition, when we averaged the DTN and DTP concentrations, the total biomass and the biomass of the seven groups by season, DTN and DTP were both positively and significantly correlated with the biomass of the major groups. This result most likely reflects the effect of nutrients that are necessary for algal development on the phytoplankton community. Many studies have focused on the effect of nutrients on phytoplankton and found that nutrient concentrations play a crucial role in phytoplankton growth (McCauley and Downing, 1991; Seip, 1994; Teubner and Dokulil, 2002). Although we did not detect an influence of nutrients on a seasonal level, it is clear that the nutrient level had an effect on the temporal pattern of phytoplankton growth, particularly on an inter-annual scale.

Regarding the spatial distribution, the phytoplankton biomass was high in the south and low in the north (particularly in the area connecting to the Yangtze River), possibly because of greater underwater light climate and high nutrient concentration in the southern area. The phytoplankton biomass was highest at Site 8, most likely because of the location (Site 8 is at the entrance of Banghu, which is a smaller lake in Lake Poyang characterized by calm conditions) and relatively high transparency. The variation in Secchi depth may also be illustrative of the spatial distribution of the relative biomass of Cyanobacteria and Chlorophyta in Lake Poyang, which was opposite to that in the northern region. Cyanobacteria can survive in a wide range of light intensities (Oliver and Ganf, 2002; Reynolds, 1984a), whereas a low light intensity is unsuitable for Chlorophyta growth.

Conclusions

In contrast to other eutrophic lakes, such as Lake Taihu and Lake Neusiedlersee, the phytoplankton in Lake Poyang is dominated by Bacillariophyta rather than Cyanobacteria. This difference may be the result of the high variability in Lake Poyang lake levels and the limnological characteristics of both lake and river. The turbid environment causes a low light condition in Lake Poyang that results in low phytoplankton biomass. Given its high nutrient concentration and low phytoplankton biomass level, we conclude that light is the principal limiting factor in Lake Poyang. The seasonal variation in biomass is well explained by transparency, whereas nutrient increases stimulate inter-annual phytoplankton development, given that there are no substantial changes in light conditions. Light and nutrients in combination cause the spatial variation of phytoplankton in this lake.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2013.06.008.

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